

WHERE SUBSPECIES MEET.

By KARL JORDAN.

(With text-figures 48-53.)

IN a paper read at the 6th International Congress of Entomology which met at Madrid, September 6th to 12th, 1935, I dealt at some length with this subject. In March 1937 the General Secretary of the Congress informed me that 400 pages of the *Transactions* had been printed before war broke out and that the other manuscripts were set up in type. No progress has been made since. The General Secretary being involved in the clash of factions, it is most unlikely that the *Proceedings* and *Transactions* of the 6th Congress will be published before the end of the struggle in Spain. As my investigations of 1936 into the subject were a continuation of those recorded in the Congress paper, I repeat here some of the earlier observations before referring to my later results.

Innumerable species live side by side. However close they may agree in their morphology, there is a barrier between them which prevents interspecific promiscuity, keeping the specific populations pure. In a large percentage of species the area of distribution is subdivided into minor areas, each subarea being inhabited by a subspecific population. In those groups of animals where the systematist has advanced to the study of subspecies of the dead material at his disposal in museums, the diagnoses of subspecies are based on morphological distinctions, which are of the same kind as in the case of species. The two systematic categories being in this respect essentially alike, differing only in degree, the question arises as to whether the aversion to intercrossing which keeps the species apart also exists among the subspecies of one and the same species wherever they come into contact with one another. Where this aversion does not exist, the subspecies, so closely related to each other morphologically, must be expected to hybridize and to form hybrid populations in districts of contact. And conversely, the absence of hybrid populations may be taken as evidence that the subspecies in question are kept apart by a physiological barrier as are the species. Such conclusions may, in a given instance, be correct or not, being based on the evidence of circumstances which are not known in their entirety. Field researches and experimental breeding will have to supplement the investigations of the museum's systematist in order to make the results conclusive.

A most suitable subject for this kind of research in Europe is the widely distributed mouse-flea, *Ctenophthalmus agyrtes* Heller 1896, which is common on *Apodemus sylvaticus* and *Evtomys glareolus* and has developed into a number of subspecies. The species offers the student the great advantage that the differences between the subspecies are structural and definite, at least in the male. Moreover, a survey with the object of ascertaining the exact distribution of each subspecies of this flea would also be a survey of the fauna of mice, extensive collecting thus obtaining results in two classes of animals. I have collected most of the subspecies of *Ctenophthalmus agyrtes*; but it was only in 1931 that I for the first time devoted my holiday to obtaining an answer to the question: where do subspecies of *Ct. agyrtes* come into contact with one another? I concentrated on trapping mice; collecting other hosts and other fleas was

incidental. The fleas were studied at the hotel, so as to be certain of the progress of the investigation. The distribution of the three subspecies concerned was known at that time to be as follows :

(1) The central European *Ct. agyrtes agyrtes* Heller 1896.—Norway, Denmark, Germany, southward to the Lake of Geneva and westward to Seine Inférieure.

(2) The north-western *Ct. agyrtes nobilis* Roths. 1898 (= *Ct. a. celticus* J. & R. 1922).—Great Britain and Ireland, Brittany and southward to the Puy-de-Dôme district and Charente.

(3) The French alpine *Ct. agyrtes provincialis* Roths. 1910.—Valescure, Hautes Alpes, Zermatt and Bex-les-Bains in the Swiss Rhône valley.

My first investigation aimed at the discovery of the districts where *Ct. a. agyrtes* and *Ct. a. provincialis* meet. As I had previously collected *agyrtes* above Montreux and *provincialis* at Bex-les-Bains, I expected to find both subspecies somewhere in between the two places. I went in the spring, which proved to be a mistake; mice were very rare from Villeneuve, at the upper end of the Lake of Geneva, to Aigle, while slugs and snails abounded and sprung the traps. At Villeneuve I found only *Ct. a. agyrtes*; but at Aigle, a little east of the town, on the left side of the river coming down from Les Ormondes, I obtained *Ct. a. provincialis*; and much higher up the right bank of the Rhône valley towards Leysin, the only specimen caught was a ♂ intermediate between the two and suggesting that the plateau north of the main chain of the Bernese Oberland is inhabited by a special intermediate subspecies or by a hybrid race. We have no fleas from these higher districts of Vaud and Valais; on the north side of the mountains *Ct. a. agyrtes* is found. Poor as the results of several weeks' trapping were, they proved that the two subspecies meet round about Aigle. A renewed comparison of the fairly extensive material from Bex with the specimens from Zermatt and the French Alps has shown us that some of the Bex males are less typical, inclining a little towards *Ct. a. agyrtes*, which agrees with the suggestion that the two subspecies hybridize.

On the south side of the lake I collected at La Roche-sur-Foron, where I found only *Ct. a. agyrtes*, while in the Chamounix district only *Ct. a. provincialis* was obtained, in evidently typical specimens. The two fleas probably come into contact on the escarpment from the lower to the higher level, and good centres for this investigation would be Servoz in the Arne valley and St. Germain in the Montjoie valley. On the south side of the Col de Bonhomme *Ct. a. provincialis* may be expected to occur at higher altitudes (as it does on the north side), and *Ct. a. verbanus* J. & R. 1920 farther down. Courmayeur would appear to be a convenient place for trapping up and down the Dora Baltea in search of the two subspecies.

As stated above (p. 104), two subspecies were known from Northern France, and it was evident from the occurrence of the one in Seine Inférieure and the other in Brittany that their areas of distribution must meet somewhere in Normandy, and Bagnoles-de-l'Orne, nearly in the centre of Normandy, seemed indicated as a good starting-point for the investigation. Trapping behind the bathing establishment on a wooded knoll covered with boulders produced *Ct. a. agyrtes*; but outside the wood, in the hedges and meadows, I found *Ct. a. nobilis*. The results remained constant during the fortnight's stay in the place; only *agyrtes* in the wood and only *nobilis* in the open country: a few hundred yards

from the wood to the nearest trap in a hedge. The intermediate ground was occupied by houses and gardens where I could not put up any traps. The restriction of the two subspecies each to a definite biotope at Bagnoles is interesting and instructive. If the specimens had not been studied on the spot, but been labelled in the usual way with locality, date and host, and then been examined at home, the fact that the two insects are separate in space at Bagnoles would have been concealed. The areas of distribution do not overlap, but dovetail. Whether that is so in other districts of Normandy remains to be ascertained. There is no indication in the morphology of the Bagnoles specimens that intercrossing occurs.

Ct. a. nobilis was found by Mr. J. F. Cox at Ruffec, Charente, and in the Puy-de-Dôme district in 1931, and the Hon. Miriam Rothschild obtained it at Royat-les-Bains. In these districts it occurs together with another flea, *Ctenophthalmus arvernus* Jord. 1931, which is nearly related to *Ct. agyrtes*, but evidently specifically distinct. Miss Rothschild found the two insects actually on the same host at the same spot. There is no trace of hybridization in the fairly long series obtained.

As we had no collections from farther south and west in France, we did not know what happens to *Ct. agyrtes* south of the Auvergne. Does *Ct. a. nobilis* occur there or is it replaced by another subspecies? To provide an answer to this question I visited South-west France in 1936, selecting four widely separate places at which to spend some time: Figeac (Lot), Brassac (Tarn), St. Jean-Pied-de-Port (Basses Pyrénées) and Gavarnie (Hautes Pyrénées).

As I had found in North Spain, in 1935, a subspecies of *Ctenophthalmus agyrtes* which is in some details nearer to *Ct. a. agyrtes* than is *Ct. a. nobilis*, I expected to discover in one or the other of these French localities a race like the Spanish one or intermediate between it and *Ct. a. nobilis*, and was much surprised that I obtained no subspecies of *Ct. agyrtes* at all, but only *Ct. arvernus* in all four places. I have certainly not covered the whole country, and there exist possibly pockets between the Auvergne and the Pyrenees where *Ct. a. nobilis* may occur; but so much is certain that the ordinary flea of *Apodemus* and *Evotomys* in South-west France is *Ct. arvernus*, which takes here the same place in the fauna as *Ct. a. nobilis* in Brittany and Great Britain and *Ct. a. agyrtes* in Central Europe. A connection between the area of *Ct. a. nobilis* and that of the Spanish subspecies may be discovered to exist along the coast of the Bay of Biscay; or the pine woods of Les Landes may harbour a race of their own. We do not know. Our knowledge of the distribution in Europe, not only of fleas but of large numbers of other animals, is so meagre and it would be in many instances so easy to fill in the lacunae that I here appeal to local naturalists to take an interest in this kind of research. I suppose it is too much to hope for a well-organized survey of the fauna of Western and Central Europe.

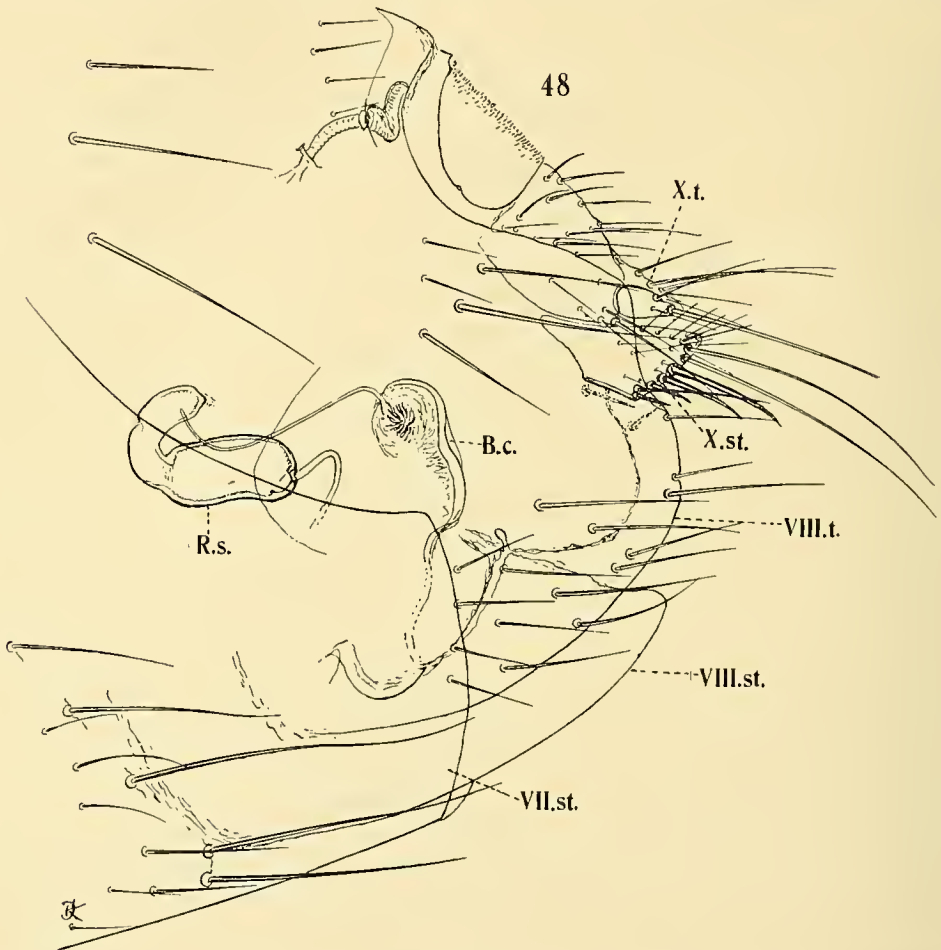
I append here the list of Siphonaptera collected in South-western France, to which is added the description of the Spanish race of *Ctenophthalmus agyrtes* above referred to, and that of another flea from Sardinia.

Collecting was concentrated on *Apodemus sylvaticus*, *Evotomys glareolus* and *Talpa europaea*. As the Spanish race occurs on the Mole, there was a possibility that the same or a similar race of *Ct. agyrtes* was parasitic on *Talpa* in the Pyrenees; the result was negative. Shrews were taken incidentally, but there were hardly any fleas on them, which was contrary to the usual experience.

No attempt was made to obtain a large and varied collection; nevertheless, several subspecies and one species are new to science. Some of the mice collected are still rare in museums. The specimens from Figeac, Brassac and St. Jean-Pied-de-Port were collected in June and those from Gavarnie and neighbourhood in July.

1. *Citellophilus occidentis* sp. nov. (text-fig. 48).

Gave d'Ossoue, Gavarnie, 1,460 m., 13. vii. 1936, on *Microtus nivalis aquitanicus*, one ♀.—The mouse was caught in a place where *Eliomys quercinus*



occurred; this is possibly the true host of the new flea. The only example of *Eliomys* caught was dead in the trap, and there were no fleas on it.

♀. Somewhat aberrant in this genus. *C. danubianus* Roths. 1909 is geographically the nearest species we have in the collection. The new species differs from it particularly in having 3 antepygial bristles, no row of bristles on the outer surface of mid- and hindfemora, a small stigma on tergite VIII, and a long body and short tail to the spermatheca. In Wagner's Catalogue of the Palaearctic fleas *C. danubianus* is placed as a synonym of *C. simplex* Wagn. 1902; but this can hardly be right, if Wagner's figures are absolutely correct as he affirms. The digitoid of *C. danubianus* bears a spiniform bristle not shown

in Wagner's figures and the other bristles of the digitoid are much longer in his figures than in our specimens of *C. danubianus* from Rumania and Bulgaria.

Rostrum extending to middle of trochanter, shorter than in *C. danubianus*. In front of eye a row of 3 long bristles, no other bristles on frons; on occiput a long bristle above middle of antennal groove, subapical row widely interrupted above the long bristle placed at the lower angle, above the wide interspace only 2 or 3 bristles in the row each side. Eye with hardly any pigment except at periphery (accidental?). Bristles of segment II of antenna much longer than club.

Pronotal comb with 19 spines inclusive of a small ventral one. On mesonotum a posterior row of 10 long bristles (the two sides together) and a row of 11 small ones, no further lateral bristles except at anterior margin, and a row of 3 or 4 dorsal ones a short distance behind the basal ones, on inner surface 11 bristle-like spines; on mesopleura 7 long and longish bristles and anteriorly 10 or 12 small ones. Bristles on metanotum 15, 10; on metepimerum 6.

Apical spines on abdominal terga (the two sides together): I 3, II 4, III 3; bristles in two rows, no additional dorsal bristles: I 13, 10, II 10, 15, III 9, 14, IV 7, 14, V 7, 14, VI 8, 13, VII 4, 12; on sterna: II 0, 2, III 0, 7, IV, 0, 8, VI 0, 8, VII 12, 10.

Apart from the subapical subventral bristle, on outer surface of forefemur 8 lateral bristles (and 2 near apex), on inner surface 2 lateral ones; on midfemur on outside no lateral bristles, on inside a row of 5; on outside of hindfemur no lateral bristles, on inside a row of 7 on one femur and 9 on the other. On hindtibia 7 dorsal notches (inclusive of apical notch), third notch with a single heavy bristle, between fifth and sixth a single subdorsal heavy bristle; on outer surface of hindtibia 9 dorsolateral bristles, including an apical one; the longest apical bristle of segment II of hindtarsus reaching to apex of III; in all tarsi of *C. danubianus* segment V with 2 apical ventral bristles and proximally of them 1 or 2 similar but smaller bristles, these latter absent in the new species. Three antepygidial bristles, upper one $\frac{3}{8}$ of middle bristle, lower one $\frac{3}{4}$, approximately.

Modified Segments.—Sternum VII narrowing apicad, the upper margin slanting-incurved (text-fig. 48, VII st.), apex broad, rounded-truncate, upper apical angle a little over 90°. Above stigma of VIII t. 3 bristles each side; stigma much smaller than in *C. danubianus*, below stigma 2 short and 3 long bristles, on lower portion of outer surface 17 bristles, inclusive of those at apical margin, on inner surface 2. Sensillum measured dorsally shorter than its distance from stylet. Some of the bristles of anal sternum (X. st.) stout and curved. Spermatheca (R.s.): body twice as long as broad, almost of even width, ventrally concave, dorsally convex, orifice terminal-subdorsal, tail measured in a straight line a very little shorter than body; bursa copulatrix with conspicuous glandular tissue, as in *C. danubianus*, blind duct long.

Length 3.0 mm.; hindfemur 0.48 mm.

2. *Nosopsyllus fasciatus* Bose 1801.

Brassac, on *Apodemus sylvaticus*, 1 ♂, and on *Mus musculus*, 1 ♂.

3. *Ctenophthalmus arvernus* Jord. 1931 (text-fig. 49).

Figeac, a series on *A. sylvaticus* and *Evotomys glareolus*.—The best collecting ground at Figeac was a steep damp lane above the railway, with rank

vegetation and a hedge each side. Here the two mice and *Crocidura russula* were rather abundant. On the dry higher ground of each side of the valley hardly any mice were found; but I obtained on the right side well above the town a specimen of *Pitymys pyrenaicus*, the second record of the species from Central France.

Brassac, a series on *A. sylvaticus* and *E. glareolus*, and 1 ♂ on *Mus musculus*.

St. Jean-Pied-de-Port, on *A. sylvaticus*, a small series.—Mice were very scarce; the hills too dry and the valley too populated. No *Evotomys* were found.

Gavarnie, on *A. sylvaticus*, 2 ♂♂, 1 ♀.—Only one specimen of this mouse was trapped and no *Evotomys*.

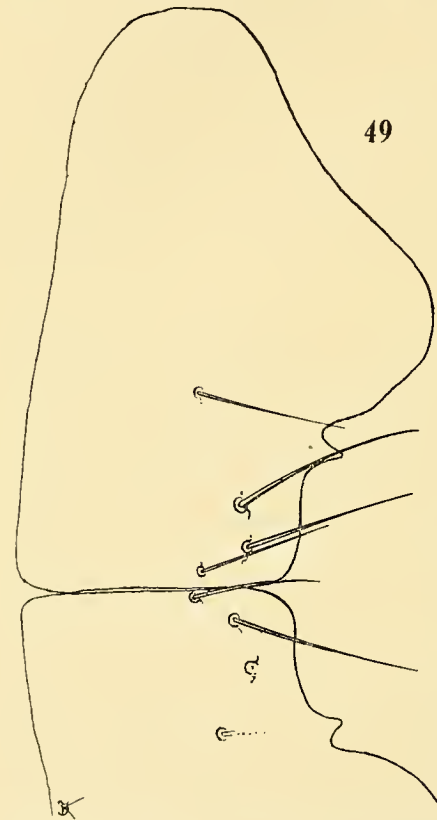
Gave d'Ossoue, above Gavarnie, on *Pitymys pyrenaicus*, 4 ♂♂, 2 ♀♀.—One specimen of this mouse taken in a mole run.

The marginal projection of VII. st. of ♀ is always short (text-fig. 42, the segment spread out), in *Ct. a. nobilis* twice as long or over.

4. *Ctenophthalmus nivalis nivalis*

Roths. 1909.

Gave d'Ossoue, above Gavarnie, on *Microtus nivalis aquitanicus*, 1 ♀.—As sternum VII of the specimen is injured, I cannot say with certainty whether the specimen agrees in this segment with *Ct. nivalis nivalis* from the Hautes Alpes and Haute Savoie. I obtained only two Snow Mice; one, without fleas, was trapped among the large boulders a short distance beyond the first bridge over the brook, the other at the other side of the water in



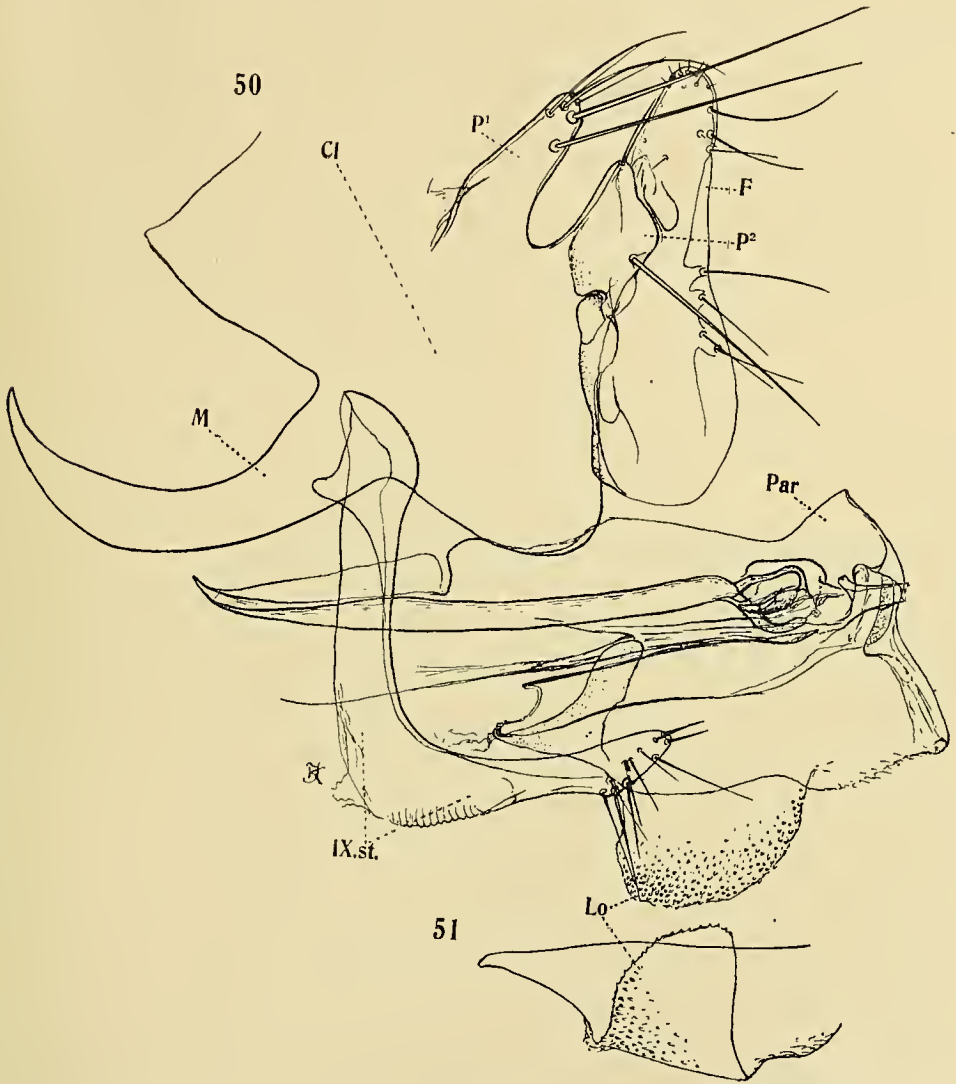
the wood near a meadow beyond the second bridge.

5. *Ctenophthalmus agyrtes hispanicus* subsp. nov. (text-fig. 50).

A single ♂ from the nest of *Talpa*, near Lake Enol, above Covadonga, Asturia, 3 Sept. 1935.—Mole-hills were plentiful in a meadow, and here and there the feet of cattle had sunk into the ground, a sure sign that there was a nest underneath. I took several nests, but contrary to my expectation (and usual experience) there were no flea-larvae in them and only one imago; the ground had been perhaps too wet.

♂. Nearest to *Ct. a. nobilis* Roth. 1898, but differing in the genitalia, particularly in the ventral lateral lobe of the phallosome. Manubrium (M) of clasper strongly curved upwards, nearly as in *Ct. baeticus* Roth. 1910 from Portugal. The ventral rounded corner of clasper more projecting downwards than in *Ct. a. nobilis* and its lowest point farther distant from digitoid F. Process P² of clasper obliquely truncate-sinuate as in some specimens of *Ct. a. nobilis*,

the posterior angle but little projecting; in the majority of French specimens of *Ct. a. nobilis* the apex of P^2 is more deeply incurved, the lower angle therefore projecting considerably; this is also the case to the same extent in a minority of British specimens, an indication of the commencement of subspecific separation. Ventral, horizontal, arm of sternum IX as narrow as in *Ct. a. nobilis*, but its ventral margin feebly angulate at some distance from tip at the point

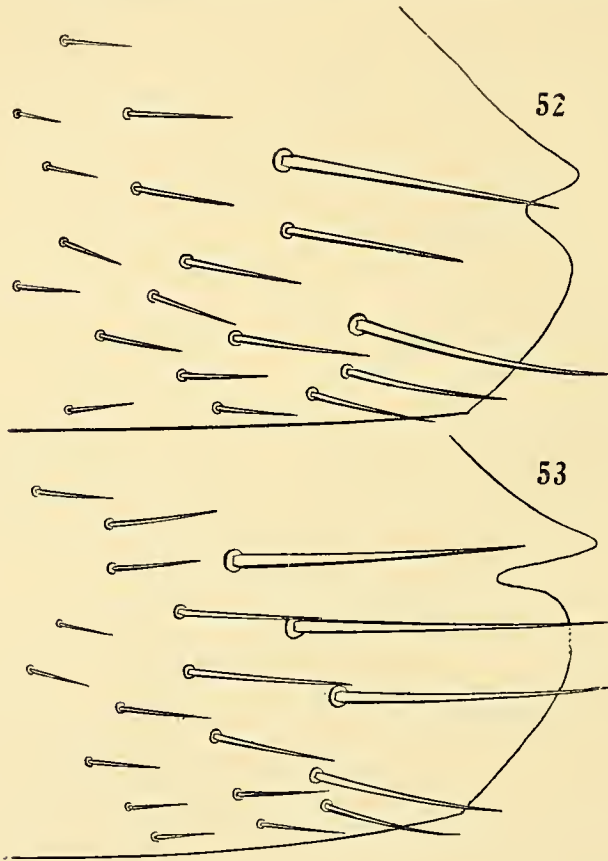


where there is a cluster of bristles. Phallosome with large, rounded, ventral flap each side (Lo), densely covered anteriorly and ventrally with semioval, somewhat scale-like, swellings directed frontad; in *Ct. a. nobilis*, on the other hand, the flap is turned upwards (occasionally turned down in mounted specimens) and its upper margin very distinctly denticulate (text-fig. 51); *nobilis* differs therein from all other subspecies of *Ct. agyrtes*, and from the purely morphological point of view therefore has some claim to specific distinctness.

6. *Rhadinopsylla mesa* Jord. 1920.

Gave d'Ossoue, Gavarnie, 1,460 m., 13.vii.36, 1 ♂ on *Talpa europaea*.— The specimen differs slightly from the only Swiss ♂ (the type) we have; the difference is either individual or geographical; at least one more ♂ is necessary for a tentative decision. The genal comb of the Pyrenean ♂ consists of 5 spines on each side; in the Swiss ♂ there are 5 spines on one side and 6 on the other; in our two Swiss ♀♀ 6 on each side. The uppermost spine of this comb is, in the Pyrenean ♂, very little broader at the base than the lowest spine and a trifle longer, not shorter as in the Swiss ♂.

In the Key to the species of *Rhadinopsylla* published in NOV. ZOOL., xxxv,



pp. 183, 184 (1929) it is stated under **a**¹ that the bristles of VIII. st. are apical in *Rh. isacanthus*; it should read subapical, the row of bristles being placed some distance from the apical margin.

7. *Typhloceras favosus rolandi* subsp. nov. (text-fig. 52).

Basses Pyrénées: St. Jean-Pied-de-Port, 150 m., on *Apodemus sylvaticus*, 28.vi.36, one ♀.

♀. Agrees with our two Algerian ♀♀ in the eye being smaller than in *T. poppei* Wagn. 1903, thorax and abdomen more distinctly reticulated, bristles of metanotum less numerous, many of the bristles of the body less pointed, the interspace between eye and upper genal spine broader than third genal spine,

hindtibia with about 25 lateral bristles (in *T. poppei* over 40). The Pyrenean specimen differs from the Algerian ones in the pronotal comb containing 22 spines instead of 20, and in the sinus of sternum VII not being deeper than in *T. poppei*: triangular lobe above this sinus narrower than in *T. poppei* (narrower on right side than on left figured) and not longer than lower lobe, which is broad and rounded (text-fig. 52).

8. ***Typhloceras favosus asunicus*** subsp. nov. (text-fig. 53).

The above-described subspecies is connected with *T. favosus favosus* J. & R. 1914 by an intermediate one from Sardinia, of which we have also but one ♀, collected by Dr. A. H. Krausse at Asuni off a mouse (and mentioned in Nov. Zool., xxi, p. 236 (1914)). Pronotal comb with 22 spines as before. Sinus of sternum VII narrow (text-fig. 53), the lobe above it decidedly longer than the broad lower lobe and twice as long as in the preceding subspecies, but one-third shorter than in *T. f. favosus*, in which the lower lobe, moreover, is nearly as long as the upper. As VII. st. is injured on the left side, we figure the right side; the long bristles are the same on both sides.
